

# Recent Disappearance of the Benthic Amphipod, *Diporeia* spp., in the Great Lakes: Spatial Patterns, Potential Causes, and Ecological Implications



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## **Abstract**

Over the past several decades, the once abundant benthic amphipod *Diporeia* spp. has completely disappeared from areas < 90 m in water depth in all the Great Lakes except Lake Superior. This organism may presently still be found in deeper areas (> 90 m), but abundances even in these areas are in a state of decline. Declines were first observed in the early 1990s, just a few years after two invasive mussels, *Dreissena polymorpha* (zebra mussel) and *Dreissena rostriformis bugensis* (quagga mussel) became established. While the spatial and temporal decline of *Diporeia* coincided with the expansion of these two mussel species, the exact reason for the negative response of *Diporeia* to *Dreissena* has not been clearly defined. In the Great Lakes, the rate at which the population disappeared has varied from months to many years, and has occurred in areas remote from mussel-infested regions. The loss of *Diporeia* is having a far-reaching impact on the Great Lakes food web. As *Diporeia* is a benthic detritivore that was heavily fed upon by fish, this calorie-rich organism provided an efficient pathway by which energy produced and settled from the pelagic region (primary production) was cycled to upper trophic levels. With the loss of *Diporeia* and the recent expansion of *D. r. bugensis* into both nearshore and offshore regions, the benthic community has become an energy sink rather than a pathway. As a result, the abundance, growth, and condition of fish populations are declining.

## **Introduction**

The benthic amphipod *Diporeia* spp. is part of a relic faunal group that mostly inhabit deep, cold pro-glaciated lakes, brackish estuaries, and coastal margins in the Holarctic region (Bousfield 1989). In North America, it is found in deep, boreal lakes from the lower Mackenzie River in the west to Lake Champlain in the east where near-bottom summer temperatures do not exceed 14 °C (Dadswell 1974). More specifically in the Great Lakes, *Diporeia* (actually a species complex) was the dominant benthic organism in deeper regions (> 30 m) of all the lakes, comprising over 70 % of benthic biomass in these regions (Nalepa 1989). It was present but less dominant in open, shallow regions of the main lake basins (< 30 m), and naturally absent from shallow, warm bays and basins. *Diporeia* has a life span of up to 2-3 years, and reaches a maxi-

Image of the benthic amphipod *Diporeia* spp. Mean body length in Lake Michigan is about 10 mm.



mum size of about 10 mm (Fig. 1).

As a detritivore, it burrows in the top 1-2 cm of sediments and mostly feeds on organic material that settles from overlying waters. In particular, *Diporeia* feeds heavily on diatoms that settle during the spring bloom period. Diatoms are an energy-rich phytoplankton group, and ingestion rates, energy stores (lipids), and growth rates of *Diporeia* reached a seasonal peak during or just after the spring bloom (Gardner et al. 1985, 1990, Dermott and Corning 1988). In turn, *Diporeia* was fed upon by many fish species, including the commercially important lake whitefish, and forage fish such as alewife, bloater, and sculpin that serve as prey for larger piscivores (salmon, trout) (Scott and Crossman 1973, Wells 1980). Thus, *Diporeia* played a major role in the efficient movement of energy between lower (diatoms, phytoplankton) and upper (fish) trophic levels and was considered a keystone species in the Great Lakes ecosystem.

Over the past several decades, this once widespread, abundant organism has totally disappeared from large areas in all the Great Lakes except Lake Superior, and abundances of remaining populations are in the state of decline (Nalepa et al. 2006a, 2009). In this brief paper, I provide the background for current trends, consider potential causes for the decline, and summarize realized and potential ecological consequences.

### Historical Perspective

A sufficient number of historic surveys have been conducted in the Great Lakes to conclude that the current wide-scale disappearance of *Diporeia* is unprecedented. Previous studies of temporal trends over both the long (decades) and short term (years) show that populations do fluctuate relative to environmental conditions, but the total, systematic loss of entire populations over large areas is unique. Historically, long-term trends were mostly related

to changes in nutrient loads and pelagic productivity (Robertson and Alley 1966, Cook and Johnson 1974, Nalepa 1987). Nutrient loads (phosphorus) from both point and non-point sources increased up until the mid-1970s, leading to greater standing stocks of phytoplankton and hence greater amounts of organic material settling to the bottom. This material served as food for *Diporeia* and, as a result, *Diporeia* abundances increased. For example, in Lake Michigan at depths < 50 m, densities increased 2-fold between the 1930s and the mid-1960s (Robertson and Alley 1966), and 2 to 5-fold between the 1960s and the early 1980s (Nalepa 1987). After nutrient abatement programs in the mid-1970s, abundances declined consistent with diminished food availability (Nalepa et al. 1998). Shorter-term fluctuations have also been documented and mostly attributed to shifts in fish predators. In the Bay of Quinte, Lake Ontario, the *Diporeia* population in the late 1970s/early 1980s rapidly increased to levels more typical of those found in this portion of eastern Lake Ontario (Johnson and McNeil 1986). The population increase was related to the collapse of large populations of white perch which heavily fed on *Diporeia* and suppressed their numbers. In Lake Michigan, short-term changes in abundances were also attributed to population shifts in fish predators (McDonald et al. 1990). In each of these cases, it should be emphasized that *Diporeia* was still present, but abundances were simply lower than typically found; recovery occurred rapidly once predation pressure eased.

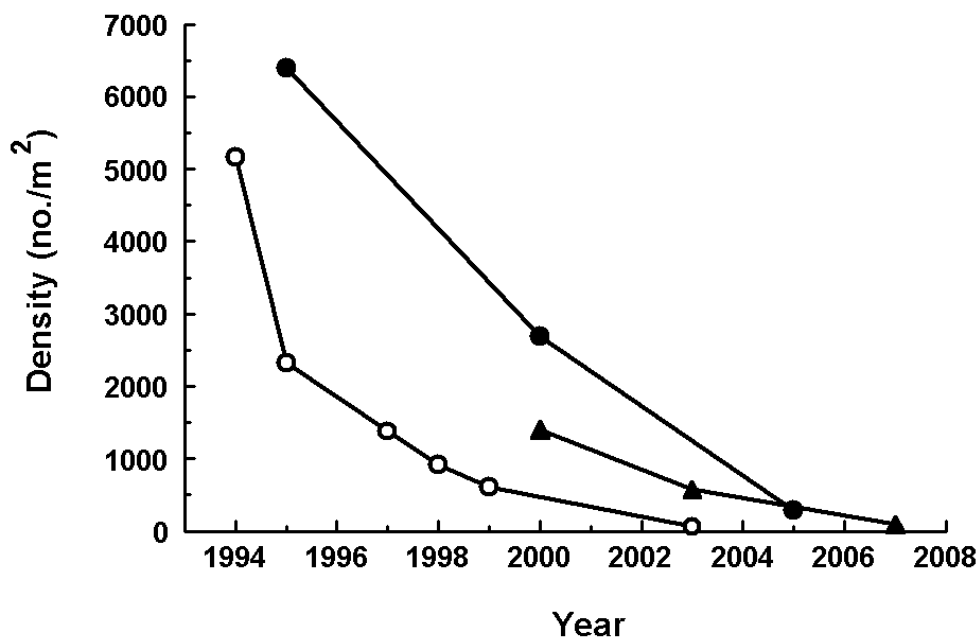
### Recent Declines

Beginning in the early 1990s, *Diporeia* populations began to decline and eventually disappear from large areas, including southeastern Lake Michigan, outer Saginaw Bay, eastern Lake Erie, and eastern Lake Ontario (Dermott and Kerec 1997, Dermott 2001, Lozano et al.

2001, Nalepa et al. 2003, 2006b). Initially, the decline was focused in near-shore areas (< 50 m), but over time progressed to deeper areas as well. In each lake area, the decline coincided with the introduction and spread of two invading bivalve mollusks, *Dreissena polymorpha* (zebra mussel) and *Dreissena rostriformis bugensis* (quagga mussel). The chronology of the *Diporeia* decline relative to the expansion of *Dreissena* was well-documented in Lake Michigan. Declines in the *Diporeia* population were first observed in the southern portion of the lake in the early 1990s, a few years after *D. polymorpha* colonized that region in 1989 (Nalepa et al. 1998). Abundances of *Diporeia* continued to decrease in the 1990s as *D. polymorpha* spread throughout the lake at depths < 50 m. By 2000, *Diporeia* was rare or completely extirpated from these shallower depth regions in the far southern and northern portions of the lake, and along the eastern shoreline (Nalepa et al. 2006b). The other dreissenid species, *D. r. bugensis*, became established in the lake in 1997, and proceeded to colonize deeper regions of the lake where *D. polymorpha* was never found (> 50 m), and to attain higher densities than *D. polymorpha* in shallow regions (< 50 m) (Nalepa et al. 2001, 2009). Consequently, the *Diporeia* population continued to decline throughout the 2000s, with declines most evident at depths > 50 m. Similar patterns of decline relative to *Dreissena* expansion were observed in Lakes Ontario and Huron. Based on the most recent lakewide surveys, the *Diporeia* population at 30-90 m declined 96 % between 1995 and 2005 in Lake Michigan, declined 99 % between 1994 and 2003 in Lake Ontario, and declined 93 % between 2000 and 2007 in Lake Huron (Fig. 2). In Lake Erie, the population began to decrease in deeper regions (> 20 m) of the central and eastern basins in 1992, and was completely gone from the lake by 1998 (Dermott

**Figure 1:**

Temporal trends in density (no./m<sup>2</sup>) of the amphipod *Diporeia* based on latest surveys in Lake Michigan (Nalepa et al. 2009), Lake Ontario (Watkins et al. 2007), and Lake Huron (Nalepa et al. 2003, Nalepa unpublished data). Densities given as the mean value at a depth of 30-90 m in each lake. Lake Michigan = solid circle, Lake Ontario = open circle, Lake Huron = solid triangle (from Nalepa et al. 2009).



and Kerec 1997, MacDougall et al. 2001). Presently, *Diporeia* abundances in Lake Superior are stable, likely because *Dreissena* populations are relatively low and mainly confined to the far western portion of the lake (Scharold et al. 2004).

While the decline of *Diporeia* clearly coincided with the expansion of *Dreissena* in the Great Lakes, some aspects of its disappearance relative to *Dreissena* are inconsistent and not easily explained. For instance, at a 45-m site in southeastern Lake Michigan, *Diporeia* densities declined from 10,000/m<sup>2</sup> to near 0/m<sup>2</sup> in just 6 months in 1992 (Nalepa et al. 1998). This rapid rate of decline occurred despite the fact that *Dreissena*, although present at shallower depths, was not present at the site itself. In contrast, it took 16 years for *Diporeia* to disappear at a 20-m site in southwestern Lake Michigan, even though *Dreissena* was present at the site over the entire 16-year period (1992-2008).

*Diporeia* typically declines not only in areas where dreissenids are present, but also in areas that are far-removed from dreissenid populations (Dermott 2001, Nalepa et al. 2003, 2006b, Watkins et al. 2007).

#### Potential Causes for the Decline

A common hypothesis for the loss of *Diporeia* is that food availability has decreased because of the filtering activities of *Dreissena* (termed "food limitation" hypothesis). *Diporeia* feeds in the upper sediment layers, whereas *Dreissena* filter-feeds at the sediment surface. Thus, phytoplankton that settles to the bottom is likely intercepted and utilized by *Dreissena* before it actually reaches the upper sediments and becomes available to *Diporeia*. While some amphipod species that inhabit shallow bays and basins have increased in abundance since *Dreissena* became established, partly because they can feed on mussel biodeposits, in theory, *Diporeia*

does not feed on this material but is more dependent on freshly-settled phytoplankton (mostly diatoms). Because of water currents and other physical forces, the filtering impacts of *Dreissena* on phytoplankton extend beyond areas where populations are present, which would lead to subsequent declines in *Diporeia* over wide areas as observed. While plausible, there are several inconsistencies with the food-limitation hypothesis. As noted, past abundances were directly linked to pelagic productivity and amounts of food settling to the bottom. Under this scenario, present abundances should decline in direct proportion to declines in phytoplankton in areas where there are no dreissenids. This has not been the case. In eastern Lake Ontario, diatom biomass declined by 80% after *Dreissena* became established (Dermott 2001), but the *Diporeia* population, instead of declining by 80%, completely disappeared. Further, at the previously-mentioned site in southern Lake Michigan where *Diporeia* disappeared in 6 months, at least some potential food (diatoms) was still settling to the bottom as indicated by near-bottom sedimentation traps (Nalepa et al. 2006b).

If food limitation is the major cause of the decline in *Diporeia*, individuals should logically exhibit some physiological signs of starvation during the period of population loss. In *Diporeia*, lipid concentrations provide a good indicator of food availability. Levels increase after the spring diatom bloom when food inputs to the bottom are at a seasonal peak, and decline as food deprivation occurs during the summer stratification period when little food settles to the bottom (Gardner et al. 1985, 1990). Further, during food-deprivation experiments, lipid levels in *Diporeia* gradually declined over a period of several months as the animals utilized lipid stores to meet metabolic needs (Gauvin et al. 1989). Individual

lipid levels and weights were documented as the population declined in southeastern Lake Michigan in the late 1990s (Nalepa et al. 2006b). Levels initially declined, but then increased such that when the population eventually disappeared, levels were as high as, or higher, than levels found in the 1980s prior to dreissenid colonization. Moreover, individuals did not lose weight as typically found when amphipods are food deprived. If the food-limitation hypothesis is correct, then why lipids and weight did not decline as the *Diporeia* population disappeared remains unresolved. Efforts to link the decline to diseases, pathogens, and parasites have shown similar inconsistencies (Messick et al. 2004, Foley et al. 2006). Commonly, *Diporeia* disappears in areas far-removed from *Dreissena* colonies, particularly in areas with high rates of sedimentation (Nalepa et al. 2006b, Watkins et al. 2007). This suggests perhaps that a toxic substance directly or indirectly associated with *Dreissena* is being transported via currents and then deposited. In laboratory experiments, 100 % mortality was observed in *Diporeia* exposed to the cyanobacterium *Microcystis aeruginosa* (Kainz et al. 2010). This phytoplankton species produces the toxin microcystin, and blooms of this species and toxin concentrations have increased since the establishment of *Dreissena* (Vanderploeg et al. 2001, Dyble et al. 2008). Further, the incidence of type E botulism has increased in the Great Lakes since *Dreissena* became established (Perez-Fuentetaja et al. 2006). The bacterium that produces the toxin, *Clostridium botulinum* type E, thrives under anoxic conditions, such as those associated with decomposing mussel tissue or mussel biodeposits. Certainly, the susceptibility of *Diporeia* to these and other potentially toxic substances, diseases, and pathogens are in need of further study. Considering all the evidence, there may not be one fac-



tor causing the decline of *Diporeia*, but perhaps a multitude of factors, with a decline in food making organisms more susceptible to other environmental stresses (Nalepa 2006a, 2006b, Watkins et al. 2007).

Another enigma of the *Diporeia* decline relative to *Dreissena* is the coexistence of these two organisms in the Finger Lakes, New York. While *Dreissena* colonized these deep, summer-cold lakes in the mid -1990s and have attained densities comparable to those in the Great Lakes, *Diporeia* remains abundant, and has actually increased in Lakes Cayuga and Seneca (Dermott et al. 2006). A theory for their coexistence is that the two organisms have different food sources in the Finger Lakes (Dermott et al. 2006). Sediments of the Finger Lakes have an abundance of leaf material that is too coarse to be filtered by *Dreissena*. This material and associated bacteria could be available as food items for *Diporeia* since, depending upon circumstances, both detritus/bacteria and epilithic algae have been utilized as a nutritional resource (Guiguer and Barton 2002, Sierszen et al. 2006). Given the steep slopes of these lakes, the detrital material would be rapidly transported from shallow to deep, colder regions inhabited by *Diporeia*. Conceivably, the presence of at least some coarse, organic material that is nonfilterable by dreissenids may explain why *Diporeia* only gradually declined in some areas of the Great Lakes (i.e., the 20-m site in southwestern Lake Michigan).

### **Benthic Transformation of Lake Michigan: From *Diporeia* to *D. r. bugensis***

Regardless of the exact cause for the decline, recent studies have detailed how nutrient/energy flow has been disrupted in Lake Michigan as *Diporeia* decreased and *D. r. bugensis* increased (Nalepa et al. 2009, Fahnenstiel et al.

2010). Energy once efficiently cycled through *Diporeia* within the food web now resides in dreissenid mass (tissue and shell), and the benthic community now serves as an energy sink rather than a trophic pathway. In the 1980s when *Diporeia* was abundant and *Dreissena* was not yet present, mean densities of *Diporeia* at depth intervals of 16-30 m, 31-50 m, 51-90 m, and > 90 in the southern basin of Lake Michigan were 7, 171/m<sup>2</sup>, 10,677/m<sup>2</sup>, 6,459/m<sup>2</sup>, and 4,014/m<sup>2</sup> (Nalepa et al. 1998). In 2008, mean densities at the same depth intervals were 3/m<sup>2</sup>, 0/m<sup>2</sup>, 262/m<sup>2</sup>, and 796/m<sup>2</sup>, respectively (Nalepa et al. 2009).

Despite these declines, total mass of the benthic community actually increased because of the recent expansion of *D. r. bugensis*. The depth-weighted, mean biomass of *Diporeia* in the southern basin in the 1980s was 2.5 g/m<sup>2</sup>, whereas the mean depth-weighted biomass of *D. r. bugensis* in 2008 was 10.9 g/m<sup>2</sup>. Since nutrient loads and thus primary production within the lake have declined over the same period (Mida et al. 2010), how can *D. r. bugensis* achieve such high standing stocks compared to past populations of *Diporeia*? The evidence suggests that *D. r. bugensis* is physiologically more efficient than *Diporeia*, and thus able to sustain higher standing stocks at a given food level. *D. r. bugensis* has an assimilation efficiency (food assimilated relative to food ingested) that is 2 times greater than *Diporeia*, and a respiration rate that is 1/3 lower (Nalepa et al. 2009). Both of these attributes allow *D. r. bugensis* to allocate more energy to growth and reproduction, and less to metabolic maintenance. Also, *D. r. bugensis* can achieve higher standing stocks because of its feeding mode. Being an active filter feeder, *D. r. bugensis* has access to food resources within the entire water column during the unstratified period (October to May). The water column is well mixed at this time, and phytoplankton pro-

duced in upper, lighted waters is circulated to near bottom waters. On the other hand, *Diporeia* is a passive detritivore and has access to phytoplankton mostly in the spring when conditions favor material settling to the bottom.

The supposition that the benthic community has now become an energy sink is a consequence of not only the 4-fold increase in benthic standing stocks as *Diporeia* decreased and *D. r. bugensis* increased, but also a consequence of the great difference in nutritional value between the two organisms. *Diporeia* has a lipid content up to 30-40 % of its dry weight, making it rich in calories and a valued energy source. In contrast, *D. r. bugensis* has a lipid level consistently below 20 % and a relatively low energy content (Nalepa et al. 2010, McNickle et al. 2006). When feeding on a calorie-rich, readily available food item like *Diporeia*, fish maximize energetic benefits relative to expenditures. With the loss of *Diporeia*, benthic-feeding fish are switching to other food items, including *D. r. bugensis*, which do not offer the same energetic benefits. When a fish feeds on *D. r. bugensis* instead of *Diporeia*, it is acquiring 14 times less energy per wet weight mass (318 joules/g compared to 4,429 joules/g; given in McNickle et al. 2006). The relatively low energy density of *D. r. bugensis* is a result of its shell, which has no energy content but comprises up to 91 % of total mass. When ingested, the shell imposes energetic costs to the fish in terms of handling and eventual egestion, decreasing net feeding efficiency. Moreover, the shell imposes other ecological costs. The amount of energy used by *D. r. bugensis* to create the shell is unknown, but shell production comprised 37 % of total production (shell growth, tissue growth, reproduction) in *D. polymorpha* (Chase and Bailey 1999). Thus, energy is lost to the food web when the shell is produced by the mussel, and also lost when it is handled

and egested by fish.

### Impact on Fish

Recent studies in Lake Michigan and the other Great Lakes suggest that the disappearance of *Diporeia* is having adverse impacts on the fish community. For example, coincident with the loss of *Diporeia*, the condition, energy density, and abundance of lake whitefish has declined in Lakes Michigan, Huron, and Ontario (Mohr and Nalepa 2005). Lake whitefish is an important commercial species that historically fed heavily on *Diporeia*. Specifically in southern Lake Michigan, condition (i.e., weight per length) of lake whitefish declined 27 % as fish were forced to feed on alternate prey items including *Dreissena* (Pothoven et al. 2001). Populations have been further affected as fish now occupy habitats outside their preferred temperature range as they search for alternate food items (Hoyle 2005, Rennie et al. 2009). Besides lake whitefish, preyfish species such as alewife, sculpin, and bloater have also been impacted. In a study in southeastern Lake Michigan, the diet, abundance, and energy density of these fish species were examined in an area where *Diporeia* had disappeared, and in an area where, at the time, it was still present (Hondorp et al. 2005). Fish in the former area had altered feeding habits, a lower energy density, and diminished abundance compared to fish from the latter area. Consistent with the concept that *D. r. bugensis* is sequestering energy that is inefficiently transferred to fish, standing stock biomass of preyfish has declined dramatically in Lake Michigan. Total prey fish mass (wet weight) declined from 91 kilotonnes in 2005 to 31 kilotonnes in 2007, which is down from 450 kilotonnes in 1989 (Bunnell et al. 2009). Total mass decreased further to 24 kilotonnes in 2008 (C. Madenjian, USGS, personal communication). Similar declines in preyfish biomass have

been documented in Lake Huron; lake-wide biomass of deepwater demersal preyfish declined 87 % between 1994 and 2007 (Riley et al. 2008). While some argue that the decline in preyfish relative to the expansion of *D. r. bugensis* may be more coincidental than mechanistic (Bunnell et al. 2009), continued monitoring of both populations will further define how closely these trends are linked.

### Final Considerations

The decline of *Diporeia* in all the Great Lakes except Lake Superior has reached a point where this native, once-abundant organism no longer plays a significant role in the food web of these lakes. Besides having a direct impact on fish, the loss of *Diporeia* will likely have a cascading, indirect affect on other food web components as fish seek alternate food sources. Indeed, recent studies have shown that pelagic invertebrates such as zooplankton and the opossum shrimp *Mysis* are also declining (Barbiero et al. 2009, Pothoven et al. 2010). Such indirect impacts on other food web components are consistent with early simulation models predicting the consequences of a decline in *Diporeia* (Kitchell et al. 2000). While these declines may be attributed to intensive predation pressure from fish because *Diporeia* is no longer available as a food source, declines can also be attributed to lowered food availability (phytoplankton) resulting from extensive dreissenid filtering activities. As such, the ecological consequences of the *Diporeia* decline may never be fully defined.

Currently, *Diporeia* is still present at depths > 90 m in Lakes Michigan, Huron, and Ontario, but numbers are declining coincident with the continued offshore expansion of *D. r. bugensis* (Watkins et al. 2007, Nalepa et al. 2009). Typically, *Dreissena* populations increase at a rapid rate during the initial expansion phase, but then decline to levels more sustain-

able by the surrounding environment (Strayer and Malcom 2006). This has already happened in some shallow bays and basins of the Great Lakes for *D. polymorpha* (Nalepa et al. 2003, Hunter et al. 2004), and will eventually also happen in deep, offshore regions for *D. r. bugensis*. Yet even if populations of *D. r. bugensis* decline in the future, this species will still be present at some level, making it very unlikely that *Diporeia* will recover. *Diporeia* populations decline and eventually disappear even when *Dreissena* abundances are low, and even in areas far-removed from dreissenid colonies. Without *Diporeia*, future food web models and energy-flow paradigms will need to account for a benthic community structure that no longer efficiently transfers energy, and subsequently is no longer able to support the level of fish resources found in the past.

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School of Natural  
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